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*OPTICAL SENSITIZATION**

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In 1873 H. W. Vogel[1] found that a silver bromide plate which had been stained yellow with aniline red became more sensitive to green light, which corresponded to an absorption band in the spectrum of a solution of aniline red. From experiments developing this lead Vogel[2] drew the conclusion that "we are able to make silver bromide sensitive to any desired color, or to increase its existing sensitiveness for certain colors. It is only necessary to add a substance which will promote the decomposition of silver bromide and which absorbs the rays in question, letting the others pass."

From this discovery have followed the orthochromatic and panchromatic plates and the remarkable plates for aerial photography through a red screen. In fact, Mees has stated that the only limit to sensitization in the infra-red is the shortest wave-length emitted by surrounding objects in the dark. Beyond that one cannot go without fogging the unexposed film.

In spite of the remarkable technical development of the sensitization of photographic films to different wave-lengths, the theory of the process is still very much up in the air. S. E. Sheppard,[3] assistant director of research of the Eastman Kodak Company, says: "The exact mechanism of optical sensitizing is not yet clear. . . . That the optical sensitizing is connected with the photodecomposition of the dye is supported by the fact that the addition of silver ions to aqueous solutions of the dye greatly accelerates its decomposition (bleaching) by light. . . . In gaseous systems an atom of a gas such as mercury, absorbing in its series spectrum or a molecule of chlorine, absorbing in its band spectrum, becomes excited. This excited molecule can transfer the absorbed energy in a single act to another molecule, by a type of inelastic collision, whereby the assaulted molecule is decomposed. . . . A great amount of valuable technical information [in regard to dye sensitization] has been obtained and the number and efficiency of such optical sensitizers enormously increased,

but the theory of their action is still obscure. . . . If the collision hypothesis is correct, it would seem that any strongly adsorbed dye could act as a sensitizer for its own absorption band. This is not the case. Although many classes of dyes give more or less feeble sensitizing, many strongly adsorbed dyes do not sensitize. Actually only two groups of dyes are now practically employed as sensitizers, the phthalein and the polymethine or cyanine type dyes."

In a recent paper Sheppard[4] says: "It will be seen that the theories of dye sensitizing range from a physical transmission of energy to rather complex chemical reactions. It is possible that investigations of the time element, e.g., by way of intermittent exposures, may lead to some decision here, but at present it is evident that the mechanism of dye sensitizing is no better known than that of colloidal metals."

The real theory of optical sensitizers was given implicitly by Grotthuss[5] in 1818, over half a century before the phenomenon was discovered. Grotthuss showed that an aqueous solution of ferric chloride is not decomposed by light into ferrous chloride and chlorine because the chlorine would necessarily oxidize the ferrous salt to the ferric state. If one adds a substance like alcohol which can react with chlorine, the reverse reaction cannot take place. Consequently sunlight reduces an alcoholic solution of ferric chloride.

Grotthuss called alcohol a depolarizer in this case because he was considering the action of light as equivalent to that of a voltaic cell. In this case he was working with a practically colorless depolarizer and the active light was therefore the light absorbed by the ferric chloride. If he had used a colored depolarizer, it would have been activated to some extent by the light which it absorbed. If this activation makes it a sufficiently strong reducing agent to reduce the ferric chloride, we have optical sensitization.

This was pointed out in different words by the senior author[6] over twenty years ago, apparently in vain. "The Grotthuss theory requires that the sensitizers should be depolarizers. They must be decomposed by light and must either be reducing agents or must be converted into reducing agents by light. It is not necessary that the order of light-sensitiveness should be identical with that of the sensitizing power. This latter depends on the potential while the rate of decomposition depends also upon the unknown 'chemical resistance.' On the other hand, a general approximation between the light-sensitiveness and the sensitizing power is to be expected and is found. Dyes, which stain silver bromide and which are not depolarizers, directly or indirectly, are not sensitizers. Since we know that cyanine and the eosines are reduced by light, it is not surprising that reducing agents do not destroy the sensitizing power. Abney's experiment with cyanine follows at once now that we know that

light converts cyanine into a reducing agent. Instead of the action of sensitizers being a mysterious one, it is a matter of course if one applies the theory of Grotthuss."

It seems to us fairly obvious that a sensitizing dye must dye silver bromide without bleeding appreciably into gelatine, and that it or its decomposition product must reduce silver bromide when the two are exposed to light. The dye must be sensitive enough to light when adsorbed on the silver bromide to produce a latent image within the time limits set by the photographer.

It is evident, however, that this point of view is so foreign to the photographic experts that some experiments are necessary in order to show the advantage of this way of looking at things. The simplest form of experiment seems to us the best, though that is not the orthodox view. If we cut out the gelatine, we eliminate the possibility of the dye bleeding into it and forming a color screen. If we cut out the solid silver bromide we do not have to bother about adsorption. If the substitute for silver bromide is not reduced at all by light in aqueous solution, we can expose as long as we like and to as intense a light as we like, thereby increasing enormously the number of possible, sensitizing, dye solutions.

Grotthuss has already shown that light does not reduce an aqueous ferric chloride solution and we have confirmed that. It is a matter of general knowledge[7] that an aqueous solution of silver nitrate, which is free from organic or other reducing matter, is not darkened by light and we have confirmed that. We, therefore, added small amounts of dye to solutions of ferric chloride and of silver nitrate, pumped out the air, and exposed the solutions to a special carbon arc in a Fade-ometer until the dye color was destroyed completely. Metallic silver could then be recognized by the eye and ferrous salt could be detected by addition of potassium ferricyanide solution. Tests for ferrous salt were obtained with eosine, methyl violet, magenta, methylene blue, acid green, cardinal red, brilliant green, aurine, erythrosine, pinacyanol and orthochrome T bromide. With silver nitrate a precipitate of silver was obtained with magenta, methyl violet, brilliant green, methylene blue, alkali blue, acid green and cardinal red. Eosine and erythrosine could not be studied in this way because they give colored precipitates with silver nitrate, while pinacyanol and orthochrome T bromide reduced the silver nitrate before the air could be pumped out and before exposure to the arc.

Special experiments with color screens on the ferric chloride solutions showed that the reduction was due both to light absorbed by the ferric chloride and to light absorbed by the dye.

The general conclusions of this paper are:

1. All of the light-sensitive dyes caused reduction of ferric chloride solutions when these were exposed to light after addition of dye.

2. Light absorbed by the dye causes reduction of ferric chloride. These are true cases of optical sensitization.

3. Optical dyes in photography are light-sensitive dyes which are adsorbed by silver bromide without bleeding into the gelatine and which are or become sufficiently strong reducing agents to reduce silver bromide to the latent image on a suitable exposure to light.

4. The theory of Vogel's process was given implicitly by Grotthuss sixty-five years before Vogel's process was discovered.

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*REVERSIBLE COAGULATION IN LIVING TISSUE. IV**

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Lapicque[1] defines chronaxie as the time of duration of the electrical stimulus necessary to produce an effect when the applied voltage is double the minimum effective voltage necessary to produce the effect when the time of duration of the stimulus is very long. This minimum effective voltage is called the rheobase. A low chronaxie means high irritability and high chronaxie means low irritability. We are indebted to Dr. Hallowell Davis of Harvard University for advice in regard to making chronaxie measurements and to Professor H. S. Liddell of Cornell University for suggesting the work and for placing the necessary apparatus at our disposal.

While it is not known exactly how a stimulus is transmitted from the nerve to the muscle, Lapicque seems to have shown that the stimulus is transmitted only when the ratio of the two chronaxies, of the nerve and muscle, is less than two to one. By decreasing or increasing the chronaxie of the nerve sufficiently relatively to the muscle or by decreasing or in-

creasing the chronaxie of the muscle sufficiently relatively to the nerve, paralysis will occur. On the other hand increasing or decreasing the chronaxies of the nerve and muscle simultaneously will not cause paralysis. Different drugs may act differently on the chronaxies of the nerve and muscle as may be seen from table 1.

TABLE 1

DRUG	CHRONAXIE OF NERVE	CHRONAXIE OF MUSCLE
Curare, spartein	Normal	Increased
?	Increased	Normal
Strychnine	Decreased	Normal
Veratrine	Normal	Decreased

From table 1 we see that strychnine and veratrine will act as curarizing drugs if applied singly; but that stimulation of the muscle by the nerve will be possible if the two drugs are applied simultaneously.

In the paper[2] on "The Chemistry of Anaesthesia" it was shown that the effect of a coagulating agent was first to increase irritability and then decrease it. In terms of Lapicque's theory, the chronaxie should first decrease, then return to a pseudo-normal state, and later go above normal when the proteins of the system undergo a sufficient decrease in dispersion.

Experiments were tried on the muscle-nerve preparation of the frog. The preparation was placed in a hard-rubber trough and the portion separating the chambers containing the muscle and the nerve was sealed off carefully with vaseline, so that solutions could be added to the nerve chamber without coming in contact with the muscle. Both chambers were then filled with Ringer's solution. The chronaxie of the nerve was measured and found to be normal. Several drops of a ten per cent solution of lead nitrate were added to the nerve chamber. Three or four minutes later the chronaxie was twenty-two per cent below that of the initial normal values; eight minutes later it was forty-six per cent below normal, which was the minimum value observed. There was then a steady increase in the chronaxie and ten minutes later the chronaxie was only sixteen per cent below normal. A few minutes later the chronaxie was back to the normal level; but this was only a pseudo-normal state because the rheobase was much higher than the normal rheobase. The chronaxie continued to increase until the nerve was paralyzed. Qualitatively similar results were obtained with alcohol, ether, etc. After treatment with alcohol, the preparation was washed repeatedly with Ringer's solution and the changes were shown to be reversible qualitatively.

Chardot and Regnier[3] have shown that with cocaine hydrochloride solutions the final value of the diminution of the chronaxie is a function of the concentration. They note that the phenomenon is reversible and that during the narcotization there is a rise of the rheobase. Their values for the percentage depressions of the chronaxie with different concentra-

tions of cocaine hydrochloride solutions all at a pH of 6.8 are given in table 2.

TABLE 2

% CONCENTRATION	% DEPRESSION	% CONCENTRATION	% DEPRESSION
0.05	63	0.010	54
0.03	62	0.0075	43
0.015	55	0.0050	27

Experiments were made on the muscle-nerve preparation of the frog to see how the chronaxie varied with the hydrogen-ion concentration. If the chronaxie is due to the protein, there should be a maximum value at or near the isoelectric point of the protein. This should not be the case if the phenomenon is due to lipoids. If isoelectric points exist at all for lipoids, they are not of sufficient importance to be recorded in the literature and are certainly not characteristic. The experiments were made with buffer solutions of disodium phosphate and citric acid. After each experiment the nerve was washed with fresh Ringer's solution. The data are given in table 3.

TABLE 3

pH	AVERAGE CHRONAXIE	pH	AVERAGE CHRONAXIE
2.2	0.057	5.0	0.113
3.0	0.063	6.0	0.073
4.0	0.089	7.0	0.067

If the results are plotted graphically, the maximum is found to be about pH 4.8, which is within the range of the isoelectric points found for many proteins. This is conclusive evidence that the irritability of the nerve, and consequently also the narcosis, is due to changes in the protein and not to changes in the lipoids.

Lapicque and Larrier[4] have obtained similar results except that they found a maximum at about pH 4 instead of pH 4.8. One interesting thing is that they found a second maximum in the chronaxie of the frog's muscle at pH 6.0, and there is a protein, myogen, in frog's muscle which has an isoelectric point at pH 6.

The general results of this paper are:

1. On adding a coagulating solution to the nerve portion of a frog's muscle-nerve preparation, the chronaxie first decreases and then increases. The decreasing chronaxie corresponds to the increasing irritability observed on adding a coagulating agent.

2. These changes in the chronaxie are reversible qualitatively when the coagulating agent is removed.

3. On varying the pH, the chronaxie of the frog's nerve passes through a maximum at pH 4.8, which is practically the isoelectric point for many proteins.

4. Lapicque and Larrier found one maximum for the chronaxie of the

frog's muscle at pH 4.8 instead of pH 4.0 and a second maximum at pH 6, which is apparently due to myogen, a protein in frog's muscle having an isoelectric point at pH 6.

5. These results prove conclusively the accuracy of Claude Bernard's view that anaesthesia is due primarily to reversible coagulation of the proteins of the brain and sensory nerves as against the assumption by Meyer and Overton that anesthesia is due primarily to a disturbance of the lipoids.

Our thanks are given to Dr. Hallowell Davis of Harvard University, to Professor H. S. Liddell of Cornell University, and to Mr. D. T. Wilber of Cornell University for valuable advice and assistance.

* This work is done under the programme now being carried out at Cornell University and supported in part by a grant from the Heckscher Foundation for the Advancement of Research established by August Heckscher at Cornell University.

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THE CUPULA OF THE EAR

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The cupula has long been considered a definitely organized cap which surmounts a crista of the membranous labyrinth and extends freely into the ampullar space. Lang (1863) who first described this structure found it to be finely striped and made up of undulating, refracting fibres which rested upon the crista. These formed a complete network which was held in position by the two plana semilunata. This cupula he considered the most important of the structures associated with the ampulla, in fact, the end organ proper.

Hensen (1878, 1881) believed that, following the application of fixing solutions, swollen auditory hairs formed the mass of the cupula. The hairs he thought became the centers of coagulated fibres which extended the full length of the cupula. He further believed that the definite cupula did not exist in the living condition.

More recently Van der Stricht (1921), Kolmer (1927), and Shambaugh (1928) have described the cupula. While their descriptions may differ in details they picture essentially a nicely organized structure, striped and

dome-shaped, which rests upon the crista. It is penetrated by minute canals and into these the hairs of the sensory cells project.

In my studies on the ear I have used many preparations of cristae from the ear of the teleost, Ameiurus nebulosus. Only a part of the observations which bear directly upon the so-called cupula will be mentioned in this preliminary paper, others being left for more detailed consideration in a paper now in preparation. My investigations have been under the direction of Prof. G. H. Parker to whom I am indebted for valuable criticisms and suggestions.

In these studies both fixed specimens and living preparations have been employed. A cupula was usually found in an ampulla which had been subjected to the actions of fixing reagents and in a series of such ampullae there were always numerous variations in size, shape and structural appearance.

When fresh preparations were viewed under dark-field illumination there was found above the crista a material which appeared slightly more mucilaginous than the fluids of the neighboring endolymphic spaces. This substance, which filled all the region between the summit of the crista and the walls of the ampulla, had no regular shape and was in no sense definitely organized. It was for the most part transparent but many very minute, brightly shining particles were present which, in the fresh condition, exhibited Brownian movement. The greater part of this material was distal to the hair cells, the sensory processes themselves being in endolymph which appeared to be somewhat more fluid. The processes were free to move and were not held firmly in any enclosing cap.

Observations which were made upon living cristae and the associated materials, together with variations which were found in them and in fixed specimens, indicated that the cupula was not a definite structure which normally existed as a cap above the crista. It was suspected that the substance which had been observed in the ampullar space was a secreted material which, after the death of the tissue or under the influence of fixing reagents, coagulated upon the crista to form the structure known as the cupula.

To test this idea further fresh preparations of ampullae were so arranged that fixing reagents might be placed upon them while they were visible in dark-field illumination. By the careful examination of such preparations the effects of different fixing fluids were observed.

Formalin when placed upon a fresh crista produced marked changes. The minute particles which were present throughout the ampullar space seemed after a short time to enlarge noticeably. Within five minutes the sensory hairs, which had become somewhat shorter, were obscured by coagulating materials which completely filled the space between the crista and the opposite walls of the ampulla. Within ten minutes a coarsely granular material had formed about the hairs so that they could no longer

be seen. When the cupula first became distinctly visible it filled the entire space distal to the crista. After remaining for a longer time in the preservative the cupula gradually became smaller and, with complete fixation, formed a compact mass directly upon the free surface of the crista.

These observations, together with others which will be described later in the more detailed account, show that the cupula does not exist as a definitely organized structure in the living ampulla but is formed from the thinly mucilaginous fluid, presumably a secretion product from gland cells, which occupies that part of the endolymphic space between the summit of the crista and the opposite ampullar wall.

The fact that the so-called cupula is in reality only a coagulation product furnishes a plausible explanation of the differing details in descriptions which have been given. The earlier investigators who failed to find the cupula were working with fresh materials in which it existed only as a shapeless secretion. The descriptions with details varying from the network of Lang to the prisms and cylinders of Van der Stricht have perhaps had their origins due to the differing effects of various reagents employed.

The similarity in structure and function between the cupula and the tectorial membrane of the cochlea has been pointed out by several investigators. Should this analogy hold, it is possible that the tectorial membrane may prove to be not a membrane at all, but in whole or in part a coagulation product. I am now engaged in investigations by which I hope to determine the facts involved in this possibility.

Summary:

1. In fixed materials variations in size, shape, position and apparent structure of the so-called cupula are found.

2. The cupula does not exist as a definitely formed structure in the living ampulla.

3. A substance which contains many minute, shining particles, found distal to the crista, when acted upon by fixing reagents, coagulates upon the crista to form the so-called cupula.

4. The analogy between the cupula and the tectorial membrane indicates that this membrane may be a coagulation product also.

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THE CILIA OF NAPHTHYS BUCERA

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The cilia on the parapodia of Naphthys bucera are in a single row beginning on the outside of the respiratory cirrus at its base, continuing around the tip of this cirrus, on its inner side, and then extending on the body wall to the base of the neuropodium. The effective beat of the cilia is from the head of the worm toward its tail. The beating of the cilia in this way causes a current of water to flow on each side of the worm posteriorly in the groove formed by the division of each parapodium into a neuropodium and a notopodium.

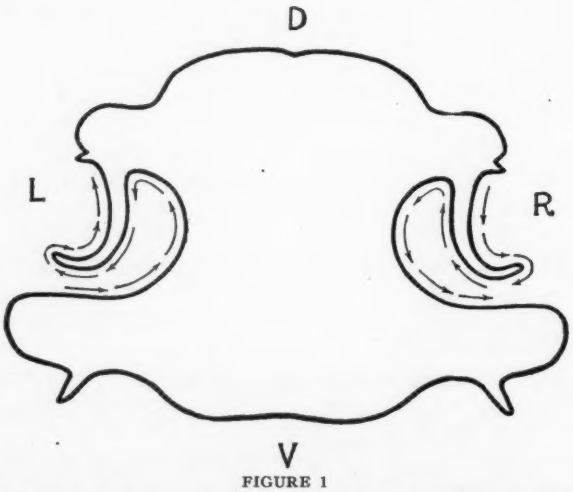

FIGURE 1

Posterior view of a cross section of the body of Nephthys showing the lines of cilia on each side and by arrows the direction of their metachronal wave. D, dorsal; V, ventral; L, left; R, right.

The metachronal wave of the cilia is at right angles to their effective beat. This wave passes from dorsal to ventral in the right side of the worm and from ventral to dorsal on its left side (Fig. 1). Thus the ciliary system exhibits a very unusual relation to the body of the worm as a whole.

A CANONICAL FORM FOR REAL MATRICES UNDER ORTHOGONAL TRANSFORMATIONS

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If $\mathbf{A}$ is a square matrix of order n with real or complex elements it is well known that it may be reduced by means of a unitary transformation $\mathbf{U}$ to a matrix of the same order all of whose elements below the leading diagonal are zero.[1] Even when the elements of $\mathbf{A}$ are real the elements of the transforming matrix $\mathbf{U}$ are complex if the characteristic numbers of $\mathbf{A}$ are not all real and it is desirable to give a canonical form which may be reached by the use of *real* unitary (i.e., orthogonal) matrices. The derivation of this canonical form differs only in detail from that given by Schur.

The characteristic numbers λ of the matrix $\mathbf{A}$ are determined by the equation $\det(\mathbf{A} - \lambda\mathbf{E}) = 0$, where $\mathbf{E}$ is the unit matrix, and they may be real or complex. If, as we suppose, the elements of $\mathbf{A}$ are real the complex roots will occur in conjugate imaginary pairs. If all the characteristic numbers are real the unitary transformations occurring in Schur's derivation will be real and the canonical form sought for is that given by Schur. On the other hand, let $\lambda_1 = \mu + i\nu$ and $\lambda_2 = \mu - i\nu$ be a pair of conjugate complex characteristic numbers of the matrix $\mathbf{A}$ (μ, ν real, $\nu \neq 0$); on denoting by $\mathbf{x}_1 = \mathbf{a} + i\mathbf{b}$, ($\mathbf{a}$, $\mathbf{b}$, real) a characteristic vector of $\mathbf{A}$ associated with the characteristic number λ_1 we have $\mathbf{A}\mathbf{x}_1 = \lambda_1\mathbf{x}_1$ which implies the two equations

$$\mathbf{A}\mathbf{a} = \mu\mathbf{a} - \nu\mathbf{b}; \quad \mathbf{A}\mathbf{b} = \mu\mathbf{b} + \nu\mathbf{a}. \tag{1}$$

It is clear that neither $\mathbf{a}$ nor $\mathbf{b}$ can be the zero vector; for if $\mathbf{a} = \mathbf{0}$ then $\mathbf{b} = \mathbf{0}$ from the first of the two equations just given and hence $\mathbf{x}_1 = \mathbf{0}$, which is at variance with the statement that $\mathbf{x}_1$ is a characteristic vector; similarly, if $\mathbf{b} = \mathbf{0}$, $\mathbf{a} = \mathbf{0}$ from the second of the two equations and $\mathbf{x}_1$ would again $= \mathbf{0}$. Furthermore $\mathbf{b}$ cannot be a multiple of $\mathbf{a}$, for then $\mathbf{x}_1' = \mathbf{a}$ would be a characteristic vector of $\mathbf{A}$ corresponding to λ_1 and we have just seen that this is impossible. Hence the two vectors $\mathbf{a}$ and $\mathbf{b}$ determine a plane and if $\mathbf{u}$ and $\mathbf{v}$ are two unit orthogonal vectors in this plane, $\mathbf{a}$ and $\mathbf{b}$ may be expressed in the form

$$\mathbf{a} = \alpha\mathbf{u} + \beta\mathbf{v}; \quad \mathbf{b} = \gamma\mathbf{u} + \delta\mathbf{v},$$

where we may, without lack of generality, assume $\alpha\delta - \beta\gamma = 1$ (since a characteristic vector is indeterminate to the extent of a scalar factor). On inserting these expressions in (1) and solving for $\mathbf{A}\mathbf{u}$ and $\mathbf{A}\mathbf{v}$ we obtain

$$\mathbf{Au} = [\mu - \nu(\alpha\beta + \gamma\delta)]\mathbf{u} - \nu(\beta^2 + \delta^2)\mathbf{v}; \quad \mathbf{Av} = \nu(\alpha^2 + \gamma^2)\mathbf{u} + [\mu + \nu(\alpha\beta + \gamma\delta)]\mathbf{v}. \tag{2}$$

If now we denote by $\mathbf{O}$ an orthogonal matrix whose columns consist, in the order given, of the components of $\mathbf{u}$ and of $\mathbf{v}$ and of n-2 other real vectors forming with these a set of mutually orthogonal unit vectors, we have $\mathbf{u} = \mathbf{Oe}_1$, $\mathbf{v} = \mathbf{Oe}_2$, where $\mathbf{e}_1$ and $\mathbf{e}_2$ are the vectors (1, 0, 0 ... 0) and (0, 1, 0 ... 0), respectively. It follows from equations (2), on denoting the matrix $\mathbf{O}^{-1}\mathbf{AO}$ by $\mathbf{B}$ that

$$\mathbf{Be}_1 = [\mu - \nu(\alpha\beta + \gamma\delta)]\mathbf{e}_1 - \nu(\beta^2 + \delta^2)\mathbf{e}_2; \quad \mathbf{Be}_2 = \nu(\alpha^2 + \gamma^2)\mathbf{e}_1 + [\mu + \nu(\alpha\beta + \gamma\delta)]\mathbf{e}_2, \tag{3}$$

and on considering the third, fourth, ... to last components of these vector equations we find $b_1^p = 0 = b_2^q$ ($p, q = 3, \ldots n$), where b_s^r denotes the element in the r^{th} row and s^{th} column of $\mathbf{B}$. Hence $\mathbf{B}$ has all elements in the first two columns, under the first two rows, zero. By properly choosing the unit orthogonal vectors ($\mathbf{u}, \mathbf{v}$) in the ($\mathbf{a}, \mathbf{b}$) plane the elements b_2^1 and b_1^2 may be made one the negative of the other. This requires $\alpha^2 + \gamma^2 = \beta^2 + \delta^2$ and if this equality is not satisfied a rotation of the ($\mathbf{u}, \mathbf{v}$) vectors through an angle

$$\theta = {}^1/_2 \arctan(\beta^2 + \delta^2 - \alpha^2 - \gamma^2)/2(\alpha\beta + \gamma\delta)$$

in their plane procures it. Proceeding in this way with the remaining pairs of conjugate complex characteristic numbers (if any) and by Schur's method with the real characteristic numbers we find as a canonical form, under orthogonal transformations, of an arbitrary real matrix $\mathbf{A}$ the form

$$\mathbf{C} = \begin{bmatrix} c_1^1 & c_2^1 & \ldots & c_n^1 \\ c_1^2 & c_2^2 & \ldots & c_n^2 \\ 0 & 0 & c_3^3 & \ldots \\ 0 & 0 & c_3^4 & \ldots \\ 0 & 0 & 0 & \ldots \end{bmatrix}; \; c_1^2 = -c_2^1; \; c_3^4 = -c_4^3, \text{ etc.} \tag{4}$$

where when, instead of a pair of conjugate complex characteristic numbers, we have a real characteristic number the element such as c_1^2 or c_3^4 is also zero. Since the characteristic numbers of a matrix are invariant under transformations of the matrix it is clear that λ_1 and λ_2 are the characteristic numbers of the *two-rowed* matrix $\begin{pmatrix} c_1^1 & c_2^1 \\ c_1^2 & c_2^2 \end{pmatrix}$, $c_1^2 = -c_2^1$ and so on.

Normal Matrices.—A matrix $\mathbf{A}$ is said to be normal when it is commutable with its transposed, i.e., $\mathbf{AA}' = \mathbf{A}'\mathbf{A}$. This property is invariant under transformation by an orthogonal matrix. On expressing the fact that $\mathbf{C}$ is normal we find[4] that $c_3^1 = c_4^1 = \; = c_n^1 = 0$; $c_1^1 = c_2^2$ and so on, so that the canonical form for normal matrices is

$$\mathbf{C}_N = \begin{bmatrix} c_1^1 & c_2^1 & 0 \ldots & & 0 \\ c_1^2 & c_1^1 & 0 \ldots & & 0 \\ 0 & 0 & c_3^3 & c_4^3 & 0 \ldots 0 \\ 0 & 0 & c_3^4 & c_3^3 & 0 \ldots 0 \end{bmatrix}; \; c_1^2 = -c_2^1, \text{ etc.} \qquad (5)$$

Since **A** is normal and remains so under orthogonal transformations, it is clear that its canonical form $\mathbf{C}_N$ consists of normal two-rowed matrices (if n is odd the canonical form also contains one "one-rowed" matrix). The transformation or invariant theory of real normal matrices with respect to the group of (real) orthogonal transformations is accordingly reduced to the case $n = 2$.

In order that a two-rowed matrix should be normal, it is clearly necessary and sufficient that it should be either symmetrical (containing three arbitrary elements) or of the form

$$\begin{pmatrix} \alpha & \beta \\ -\beta & \alpha \end{pmatrix} \qquad (6)$$

(containing only two arbitrary elements), the common boundary of the domains of these two classes being the set of diagonal matrices for which the two diagonal elements are equal, i.e., scalar matrices.

Returning to the case of an arbitrary n it is clear that the (real) symmetric, skew-symmetric and orthogonal matrices are normal and remain symmetric, skew-symmetric or orthogonal, respectively, under orthogonal transformations so that also the two-rowed matrices of their canonical forms must belong respectively to these three types. The skew-symmetric and orthogonal two-rowed matrices being characterized by the fact that they may be written in the form (6) where $\alpha = 0$ and $\alpha^2 + \beta^2 = 1$, respectively, we see that the above theorem on the canonical form of normal matrices yields, not only for the symmetric but also for the skew-symmetric and orthogonal matrices, the classical canonical forms which in the literature, for instance Weyl,[5] are not obtained by a common demonstration. We have, of course, canonical forms also for normal matrices which do not belong to these three special types. The characteristic numbers of the matrix (6) being $\alpha \pm i\beta$ it is clear from (5) that any n rowed real normal matrix is then and only then symmetric, skew-symmetric or orthogonal if all its characteristic numbers lie on the real axis, or the imaginary axis, or the boundary of the unit circle respectively (only the first part of the theorem is generally known, but from the polygon rule of Toeplitz the second part of the theorem concerning the sufficiency can be derived).

Any normal matrix **A** may be represented as the product of two commutable matrices **P** and **O** where **P** is symmetric and not-negative definite and **O** is orthogonal. Conversely any matrix **A** which may be represented

in this form is clearly normal. This product representation[6] which corresponds to the polar representation $a = pt$, $p \geqslant$ zero and $|t| = 1$, of the ordinary complex numbers a may obviously be reduced to the case $n = 2$ and in this case a simple calculation verifies the theorem.

[1] Schur, I., *Math. Annalen*, **66**, 489–492 (1909).

[2] The corresponding question for those real matrices which can be transformed by a *not necessarily* unitary matrix into the diagonal form (i.e., those having only simple elementary divisors) but which cannot be transformed into a real diagonal form has been discussed by Weierstrass in his theory of small vibrations.

[3] Toeplitz, O., *Math. Zeit.*, **2**, 187–197 (1918).

[4] Cf. Toeplitz, loc. cit.

[5] Weyl, H., *Gruppentheorie und Quantenmechanik*, 20, 23, 274.

[6] Cf. Wintner, A., *Math. Zeit.*, **30**, 280–281 (1929).

WAVE MOTION AND THE EQUATION OF CONTINUITY

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It is well known that small disturbances from equilibrium in a compressible fluid medium are propagated in accordance with the wave equation

$$\nabla^2 \varphi = \ddot{\varphi}/c^2, \tag{1}$$

where φ is the velocity potential (i.e., the function of the coördinates such that $\dot{\xi}$, $\dot{\eta}$, $\dot{\rho}$, the component particle velocities of the medium in the x, y, z directions, are equal, respectively, to $\left(\frac{\partial\varphi}{\partial x}, \frac{\partial\varphi}{\partial y}, \frac{\partial\varphi}{\partial z}\right)$, and c is the velocity of propagation. Perhaps the simplest way to deduce this equation is to consider the two fundamental equations: (A), that which expresses the essential continuity of the medium and (B), the hydrodynamic equation of motion written under the approximation appropriate to the small changes assumed. If $\delta\rho$ is the variation from the equilibrium density ρ_0, we introduce the important auxiliary quantity s, the condensation, equal to $\delta\rho/\rho_0$. We may then write

(A) The equation of continuity

$$\nabla^2\varphi = -\dot{s}\ . \tag{2}$$

(B) The equation of motion[1]

$$\dot{\varphi} = -c^2 s. \tag{3}$$

The elimination of s between (2) and (3) leads at once to equation (1). We may look upon the physical content of (1) as the combination, so to speak, of the physical contents of (2) and (3). It is perhaps worth while to emphasize that equation (3) focusses attention on the *motion* of a *part* of the medium considered to move as a whole, i.e., as a *particle* moves, while equation (2) is the expression of the fact that the motion is taking place in a *continuous* medium. Hence both ideas are implied in wave motion.

In the present paper we shall discuss several illustrations of this duality idea. Rather simple cases will be considered, but they may be readily generalized.

First take the case of the propagation of longitudinal waves in a long solid rod. Let the x axis coincide with the rod and denote by ξ the displacement from equilibrium in this direction. The *excess stress* (i.e., variation in stress from the equilibrium value) along the rod is X_e. We then have for the equation of motion for any small element of the rod, if ρ_0 is the equilibrium density,

$$\rho_0 \ddot{\xi} = \frac{\partial X_e}{\partial x}. \tag{4}$$

Now assume that X_e is a linear function of the excess density, and write

$$X_e = -c^2 \delta\rho = -c^2 \rho_0 s \tag{5}$$

with the usual definition of s. The quantity c^2 is at this stage merely a proportionality constant. The physical significance of this assumption will appear in a moment. Now the equation of continuity in this case is clearly

$$\dot{\rho} = -\frac{\partial}{\partial x}(\rho \dot{\xi}) \tag{6}$$

as may be seen by examining the "flow" through a volume element. Substituting $\rho = \rho_0 (1 + s)$ and neglecting higher order terms (6) becomes

$$\dot{s} = \frac{\partial \dot{\xi}}{\partial x} = \dot{X}_e / \rho_0 c^2. \tag{7}$$

Integrating (7) and neglecting an additive term constant in time we have

$$\frac{\partial \xi}{\partial x} = X_e / \rho_0 c^2, \tag{8}$$

which is the modified form of the equation of continuity. Elimination of X_e between (8) and (4) then yields the usual wave equation

$$\ddot{\xi} = c^2 \frac{\partial^2 \xi}{\partial x^2} \tag{9}$$

with c appearing as the wave velocity. The interesting point here is the physical significance of the continuity equation. If we write it in the form

$$X_e / \frac{\partial \xi}{\partial x} = \rho_0 c^2 = \text{const.} \tag{10}$$

it is recognized at once as *Hooke's law*, and the constant in the present example is Young's modulus, Y. Hence we have the interesting conclusion that here, as before, the wave equation results from a combination of an equation of motion and the equation of continuity, the latter appearing here in the guise of Hooke's law.

We shall not generalize this result here, but proceed to another simple illustration of somewhat different nature, namely, that of the propagation of a transverse disturbance in a flexible string. Let the equilibrium value of the tension in the string be denoted by τ_0 and the instantaneous value of the normal component by τ_n. The equilibrium line density is ρ_0. The equation of motion of an element of the string of unstretched length dx, considered to move as a whole, is approximately

$$\rho_0 \ddot{\xi} dx = \frac{\partial \tau_n}{\partial x} dx \tag{11}$$

as may be seen in the usual way. To complete the specification of the motion requires an equation which expresses the fact that the string behaves like a continuous medium. In its *simplest* form this latter equation is (approximately)

$$\tau_n = \tau_0 \frac{\partial \xi}{\partial x}, \tag{12}$$

supposed to hold *everywhere* along the string. Elimination of τ_n between (11) and (12) yields the usual wave equation for the transverse motions of a string, the velocity of propagation being $c = \sqrt{\tau_0/\rho_0}$. In this problem the equation (12) plays the same rôle as equation (8) in the case of the longitudinal motions of a rod and equation (2) in the case of compressional motions of a fluid. We may look upon it as expressing the continuity of the string as a medium for the propagation of disturbances.

We shall now examine whether we can find an illustration of the above point of view in the case of electromagnetic wave propagation. Consider the equations of the electromagnetic field in free space.

$$(a)\ \frac{1}{c}\dot{\mathbf{F}} = \nabla \times \mathbf{H}, \qquad (b)\ \frac{1}{c}\dot{\mathbf{H}} = -\nabla \times \mathbf{F}$$
$$(c)\ \nabla \cdot \mathbf{H} = 0 \qquad (d)\ \nabla \cdot \mathbf{F} = 0. \tag{13}$$

Now introduce the vector potential $\mathbf{A}$ where

$$\mathbf{H} = \nabla \times \mathbf{A}. \tag{14}$$

From equation (a) of (13) we then have

$$\frac{1}{c}\dot{\mathbf{F}} = \nabla \times \mathbf{H} = \nabla \times \nabla \times \mathbf{A}$$
$$= -\nabla^2\mathbf{A} + \nabla\ (\nabla \cdot \mathbf{A}). \tag{15}$$

Now from equation (b) of (13) we also have

$$\frac{1}{c}\dot{\mathbf{H}} = -\nabla \times \mathbf{F} = \frac{1}{c}\nabla \times \dot{\mathbf{A}} \tag{16}$$

if we employ (14) again. From (16) it follows that

$$\mathbf{F} = -\frac{1}{c}\dot{\mathbf{A}} + \mathbf{C} \tag{17}$$

where $\mathbf{C}$ is an irrotational vector. We may put it equal to $-\nabla V$, where V is the so-called scalar potential. If now we set

$$\nabla \cdot \mathbf{A} = -\frac{1}{c}\dot{V} \tag{18}$$

the relation in electromagnetic theory usually assumed between $\mathbf{A}$ and V, we have from equation (15)

$$\nabla^2\mathbf{A} = -\frac{1}{c}\dot{\mathbf{F}} - \frac{1}{c}\nabla\dot{V}$$
$$= -\frac{\partial}{\partial t}\left[\frac{1}{c}(\mathbf{F} + \nabla V)\right] \tag{19}$$

while equation (17) now becomes

$$\dot{\mathbf{A}} = -c^2\left[\frac{1}{c}(\mathbf{F} + \nabla V)\right]. \tag{20}$$

Both (19) and (20) are vector equations, i.e., they are equivalent to the scalar equations

$$\nabla^2 \mathbf{A}_x = -\frac{\partial}{\partial t}\left[\frac{1}{c}\left(F_x + \frac{\partial V}{\partial x}\right)\right] \qquad (21)$$

etc.

and

$$\dot{\mathbf{A}}_x = -c^2\left[\frac{1}{c}\left(F_x + \frac{\partial V}{\partial x}\right)\right]. \qquad (22)$$

etc.

Each pair of equations (21) and (22) is precisely in the form of the earlier equations (2) and (3) with $\mathbf{A}_x$, etc., in the place of φ and $\frac{1}{c}\left(F_x + \frac{\partial V}{\partial x}\right)$, etc., in the place of s. The elimination of $\frac{1}{c}(\mathbf{F} + \nabla V)$ between (19) and (20) leads at once to the vector wave equation

$$\nabla^2 \mathbf{A} = \frac{1}{c^2}\ddot{\mathbf{A}}, \qquad (23)$$

which in turn implies the propagation of $\mathbf{H}$ and $\mathbf{F}$ as waves with velocity c. It would seem that a certain physical significance might be attributed to the mathematical analogy indicated. However, we shall not press the matter at this point.

Generalized Canonical Equations.—The motion of any conservative dynamical system of n degrees of freedom is described by means of the $2n$ canonical equations of Hamilton, viz.,

$$\frac{\partial H}{\partial q_j} = -\dot{p}_j, \frac{\partial H}{\partial p_j} = \dot{q}_j, \qquad (24)$$

where $j = 1, 2, 3, \ldots n$ and where $H(p_j, q_j)$ is the Hamiltonian, a function of $q_1 \ldots q_n$, $p_1 \ldots p_n$. It is now an interesting question whether the equations (2) and (3) which specify the behavior of a continuous fluid medium cannot be thrown into the form of a Hamiltonian system like (24), wherein of course the Hamiltonian will have to depend on the motion in every part of the medium and hence will have to be a functional.

For the sake of simplicity, let us confine our attention to the one-dimensional case of an acoustic wave in a straight tube along the x-axis of constant cross-section S. The velocity potential φ is chosen as the fundamental variable, the "continuum" coordinate.[2] Being a function of x and t, φ has a whole continuum of values for any t as x varies along the tube. Recalling that if ξ denotes the particle displacement along the tube, $\dot{\xi} = \frac{\partial \varphi}{\partial x}$, while $\dot{\varphi} = -c^2 s$, we may write[3] for the total energy in a plane progressive wave in the tube between $x = x_1$ and $x = x_2$

$$W(\varphi, \dot{\varphi}) = \int_{x_1}^{x_2} \left(\frac{S}{2}\right)\left[\rho_0 \left(\frac{\partial \varphi}{\partial x}\right)^2 + \frac{\rho_0 \dot{\varphi}^2}{c^2}\right] dx, \qquad (25)$$

where ρ_0 is the equilibrium density of the fluid in the tube, S the constant cross sectional area of the tube and c the wave velocity. $W(\varphi, \dot{\varphi})$ must be considered as a *functional* of φ and $\dot{\varphi}$ because it depends on the *whole range* of values of φ and $\dot{\varphi}$ between x_1 and x_2. Let us call the integrand $F\left(\varphi, \frac{\partial \varphi}{\partial x}\right)$. We shall then define the *functional derivatives* of W with respect to $\dot{\varphi}$ and φ as follows:

$$\frac{\delta W}{\delta \varphi} = \frac{\partial F}{\partial \varphi} - \frac{d}{dx} \frac{\partial F}{\partial\left(\frac{\partial \varphi}{\partial x}\right)}$$

and (26)

$$\frac{\delta W}{\delta \dot{\varphi}} = \frac{\partial F}{\partial \dot{\varphi}} - \frac{d}{dx} \frac{\partial F}{\partial\left(\frac{\partial \varphi}{\partial x}\right)},$$

since the non-vanishing derivative of highest order occurring in F is of the first order.[4] Utilizing the equation (25) we then have

$$\frac{\delta W}{\delta \varphi} = -\frac{d}{dx}\left[S\rho_0 \frac{\partial \varphi}{\partial x}\right] = -\rho_0 S \frac{\partial^2 \varphi}{\partial x^2} = -\frac{\rho_0 S}{c^2} \ddot{\varphi}, \qquad (27)$$

since φ satisfies the wave equation. Also

$$\frac{\delta W}{\delta \dot{\varphi}} = \frac{\rho_0 S}{c^2} \dot{\varphi} \qquad (28)$$

To put (27) and (28) into the form of canonical equations we shall define as the continuum momentum conjugate to φ, $p_\varphi = S\rho_0 \dot{\varphi}/c^2 = -\frac{S}{c^2} p_e$ where p_e is the excess pressure. Then we have

$$W(\varphi, p_\varphi) = \int_{x_1}^{x_2} {}^1/_2 \left[S\rho_0 \left(\frac{\partial \varphi}{\partial x}\right)^2 + \frac{c^2 p_\varphi^2}{S\rho_0}\right] dx, \qquad (29)$$

whence

$$\frac{\delta W}{\delta \varphi} = -\frac{\rho_0 S \partial^2 \varphi}{\partial x^2} = -\dot{p}_\varphi \qquad (30)$$

and

$$\frac{\delta W}{\delta p_\varphi} = \frac{c^2 p_\varphi}{S\rho_0} = \dot{\varphi} \qquad (31)$$

which are now in the form of canonical equations of motion for a system of one degree of freedom with φ as coördinate and p_φ the conjugate momentum, and the quantity W acting as the Hamiltonian functional. Moreover, our choice of p_φ also assures that (30) and (31) are in the form of equations (2) and (3), respectively, and hence correspond to the equations of continuity and motion for an ideal compressible fluid. It would seem that this further emphasizes the fundamental significance of the latter equations. The result which we have established for the special case of one degree of freedom should not be difficult of extension to three or more.

[1] See, for example, Stewart and Lindsay, *Acoustics*, p. 20–23.

[2] Cf. F. Möglich, *Ann. der Phys.*, **2**, 676, 1929, some of whose analysis we shall use here.

[3] Cf. Stewart and Lindsay, *Acoustics*, p. 30, 31.

[4] Cf. Möglich, loc. cit., p. 703. In the present case the definition may be justified most simply as follows. Consider the more general expression

$$\Phi(\varphi) = \int_{x_1}^{x_2} F\left(x, \varphi, \frac{\partial\varphi}{\partial x}\right) dx. \tag{1a}$$

Now if φ is altered by $\delta\varphi$ we have

$$F\left(x, \varphi + \delta\varphi, \frac{\partial\varphi}{\partial x} + \delta\left(\frac{\partial\varphi}{\partial x}\right)\right) = F\left(x, \varphi, \frac{\partial\varphi}{\partial x}\right) + \frac{\partial F}{\partial\varphi}\delta\varphi + \frac{\partial F}{\partial\left(\frac{\partial\varphi}{\partial x}\right)}\delta\left(\frac{\partial\varphi}{\partial x}\right) + \text{higher order terms.} \tag{2a}$$

Hence if we denote the varied F by $\bar{F}$ we have

$$\delta\Phi(\varphi) = \int_{x_1}^{x_2} (\bar{F} - F)dx = \int_{x_1}^{x_2} \frac{\partial F}{\partial\varphi}\delta\varphi dx + \int_{x_1}^{x_2} \frac{\partial F}{\partial\left(\frac{\partial\varphi}{\partial x}\right)}\delta\left(\frac{\partial\varphi}{\partial x}\right) dx \tag{3a}$$

+ the integrals of terms of higher order, and if the second integral is reduced by integration by parts we have

$$\delta\Phi(\varphi) = \int_{x_1}^{x_2} \left\{\frac{\partial F}{\partial\varphi} - \frac{d}{dx}\frac{\partial F}{\partial\left(\frac{\partial\varphi}{\partial x}\right)}\right\}\delta\varphi dx + \ldots\ldots \tag{4a}$$

Then for any particular value of x

$$\frac{\delta\Phi(\varphi)}{\delta\varphi} \longrightarrow \frac{\partial F}{\partial\varphi} - \frac{d}{dx}\frac{\partial F}{\partial\left(\frac{\partial\varphi}{\partial x}\right)} \tag{5a}$$

whence the definition chosen follows at once.

ELECTRIC CONDUCTIVITY AND OPTICAL ABSORPTION IN METALS (SUPPLEMENTARY)

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NOTE: This paper is a supplement to the one which I published in the PROCEEDINGS for June, 1931. I am moved to print it now because of a correspondence which I have recently had with Doctor Swann of the Bartol Research Foundation. In the previous paper I referred to two formulas, one given by J. J. Thomson, the other by Richardson, following Wilson and Jeans, for the ratio between steady-current conductivity and light-wave conductivity in metals. I knew that these formulas gave somewhat different quantitative results in certain cases. Accordingly, for my particular purpose, I decided to give them both up and attack my problem in my own way, a very crude one. Having done so I found, much to my surprise, that, for what I call "transit" conductivity, or associated-electron conductivity, my method gives the same numerical ratios that are given by Thomson's formula for free-electron conductivity. Doctor Swann, who has given especial attention to such matters, tells me that he considers the Wilson-Jeans formula, for free-electron conductivity, more accurate than the Thomson formula. I do not challenge this opinion. I have not, in fact, undertaken to support the Thomson formula or to discredit the Wilson-Jeans formula, so far as free-electron conductivity goes. I have been using a somewhat different conception of conductivity, and I do not claim rigid accuracy for my numerical conclusions in any case. The main purpose of my previous paper was to show that the conduction electrons which optical experiments give evidence of need not be free electrons but may be associated electrons, or "transit" electrons. The main purpose of this supplementary paper is to show that transit conductivity in optical experiments is dependent upon the ratio *wave-period* ÷ *transit period* in the same general way in which, according to both the Thomson formula and the Wilson-Jeans formula, free-electron conductivity is dependent upon the ratio *wave-period* ÷ *free-path period*.

The question is how much the conductivity that appears in the equations of optics, and which I shall call κ_a', falls below the steady-current conductivity, which I shall call κ_a. The answer to this question will depend on the conception one holds as to the nature of conductivity, or of resistance.

If one thinks of resistance as acting continuously during the motion of an electron, and as proportional to the velocity of the electron, κ' should be the same as κ. Meier used this conception of resistance and was surprised when κ' proved to be smaller than κ.

On the other hand, if conduction is effected by frictionless flights of the electrons, finally terminated by collisions or captures, the duration of a flight being τ, the conductivity κ', as indicated by the work done by a given applied e. m. f. in a given time, may prove to be notably less than κ, when the flight-time τ is comparable with the complete period, t_1, of a light-wave. This is essentially the conception of conduction that

Thomson was using when he wrote the formula that appears on page 84 of his "Corpuscular Theory of Matter," and which I, using τ for Thomson's $2T$, write as $\kappa_a \frac{\sin^2(\frac{1}{2}n\tau)^2}{(\frac{1}{2}n\tau)^2}$. The same general conception holds for conduction by means of "transits" of electrons from atoms to adjacent ions.

My own method of dealing with this matter, a method which claims no high degree of accuracy, is as follows:

I conceive the immediate neighborhood of any ion within a metal to be in a condition of non-equilibrium, so that the life of any ion, as such, is very short. This implies that in the ordinary state of a metal "trains" of associated electrons are constantly darting hither and thither, one direction of motion being, when there is no impressed electric field, as probable as another. An impressed field must, in order to produce a current in its own direction, be able to affect either the length or the direction of these trains, and this implies some power of promoting or inhibiting transits, but most transits begin spontaneously and so transits may begin at any phase of a light-wave.

Let us, however, for the sake of convenience assume that the transits which we are to consider begin in groups, all those of any one group simultaneously, and that in the full period, t_1, of a light-wave the number of starting groups is $t_1 \div \tau$. We will suppose that group 1 starts when t, of the wave-field equation $X = X_0 \cos nt$, is zero, so that X at the beginning $= X_0$. The next group of transits will begin when $t = \tau$, or, since $nt_1 = 2\pi$, when $nt = n\tau = 2\pi(\tau \div t_1)$, etc., the beginnings of the groups being equally spaced in time. Let us for convenience confine the discussion, at present, to cases in which $\frac{1}{2}(t_1 \div \tau)$ is a whole number.

In the absence of any specific knowledge as to the exact way in which an impressed field of force affects the transits and does work in generating heat, I shall make use of the general principle that any small force acting for a given time on a system otherwise in equilibrium produces a departure from equilibrium proportional to the force and does an amount of work, in producing this departure, proportional to the square of the force. "Equilibrium" in the present case is a mobile one, the condition of no net transfer of electrons in any direction. Departure from equilibrium is the net current produced by the force in question.

Accordingly, the heat-producing work done during a half-wave period, from $nt = 0$ to $nt = \pi$, is represented by the following expression

$$K \cdot \frac{1}{n\tau} \Sigma \left(\int_0^{nt} \cos nt \, . \, dnt \right)^2 + \ldots + \left(\int_{\pi - nt}^{\pi} \cos nt \, . \, dnt \right)^2 . \qquad (A)$$

The constant K contains as factors X_0^2 and κ_a, the latter being the full transit conductivity for steady currents. If, for illustration, we suppose

$^1/_2(t_1 \div \tau)$ to be an odd number, it is evident that one group of transits will begin when $nt = \left[\frac{1}{2}\pi - \frac{1}{2}n\tau\right]$ and end when $nt = \left[\frac{1}{2}\pi + \frac{1}{2}n\tau\right]$, so that the integral will be zero for this group. This group will therefore contribute nothing to the heat produced. It could perhaps be argued that this failure is due to a lack of e. m. f. rather than to a failure of conductivity. This consideration will be discussed presently.

Evidently, the smaller τ is, relatively to t_1, the smaller is the relative loss of heat production due to the cause just noticed. It is equally true, though not quite so evident, that reducing τ, relatively to t_1, increases in another respect the heat-producing possibilities of the wave-fields. In fact, inspection of formula (A) shows that by making τ indefinitely small we can make the value of (A) approach as closely as we please to that of

$$K\int_0^\pi \cos^2 nt.dnt, \qquad (B)$$

which is the expression to be used if the resistance is unintermittent, as writers on optical absorption usually assume it to be.

Now the K of (B) is the same as the K of (A), containing as factors X_0^2 and the full κ_a, so that in one sense one might say that the conductivity is independent of the ratio $t_1 \div \tau$. But what we now do is to take the ratio of the heat-producing powers of the two cases represented by (A) and (B), respectively, as representing the ratio of the *effective*, or *virtual*, conductivities in the two cases. Thus we write, taking κ_a' as the apparent conductivity in case (A),

$$\kappa_a' \div \kappa_a = (A) \div (B). \qquad (C)$$

That is, κ_a' is the conductivity which, if the resistance is supposed to be unintermittent, as in (B), must be assumed in order to account for the observed value of the absorption.

I shall now deal with certain definite values of $n\tau$, and find the corresponding values of $(A) \div (B)$:

When $\tau = t_1 \div 18$, *and so* $n\tau = nt_1 \div 18 = \pi \div 9$:
$(A) = K(0.2339 + 0.1810 + 0.0996 + 0.0282) \div (\pi \div 9) = 1.555\,K.$
$(B) = K(\pi \div 2) = 1.571K;$ and so $(A) \div (B) = \kappa_a' \div \kappa_a = 0.990.$

When $\tau = t_1 \div 10$, *and so* $n\tau = nt_1 \div 10 = \pi \div 5$:
$(A) = K(0.6909 + 0.2640) \div (\pi \div 5) = 1.521\,K.$
$(B) = K_x\,1.571;$ and so $(A) \div (B) = \kappa_a' \div \kappa_a = 0.968.$

When $\tau = t_1 \div 6$, *and so* $n\tau = nt_1 \div 6 = \pi \div 3$:
$(A) = K_x\,1.500 \div (\pi \div 3) = 1.433\,K.$
$(B) = K_x\,1.571;$ and so $(A) \div (B) = \kappa_a' \div \kappa_a = 0.912.$

When $\tau =$ or $> t_1 \div 2$, and so $n\tau =$ or $> \pi$, a somewhat different procedure is necessary. I then assume six groups of transits, one group beginning when $nt = 0$, one when $nt = \frac{1}{6}\pi$, etc., the last when $nt = \frac{5}{6}\pi$. *When* $\tau = t_1 \div 2$, *and so* $n\tau = nt_1 \div 2 = \pi$: We have now for comparison

$$K \cdot \frac{1}{n\tau} \sum \left(\int_0^{n\tau} \cos nt.dnt \right)^2 + \ldots + \left(\int_{\frac{1}{6}\pi}^{\frac{1}{6}\pi + n\tau} \cos nt.dnt \right)^2, \qquad (A)$$

and

$$K \sum \int_0^{n\tau} \cos^2 nt.dnt + \ldots + \int_{\frac{1}{6}\pi}^{\frac{1}{6}\pi + n\tau} \cos^2 nt.dnt. \qquad (B)$$

Numerically, in this case,
$(A) = K(0 + 2 \times 1.000 + 2 \times 2.999 + 4.000) \div \pi = 3.821\ K.$
$(B) = K \times 3\pi$; and so $(A) \div (B) = \kappa_a' \div \kappa_a = 0.405.$

When $\tau = \frac{3}{4} nt_1$, *and so* $n\tau = \frac{3}{4} nt_1 = \frac{3}{2}\pi$:
$(A) = K\ (2 \times 1.000 + 2 \times 1.8666 + 2 \times 0.134) \div \frac{3}{2}\pi = 1.274\ K.$
$(B) = K\ (2 \times 2.356 + 2 \times 1.923 + 2 \times 2.789) = 14.14\ K.$
$(A) \div (B) = \kappa_a' \div \kappa_a = 0.090.$

When $\tau = t_1$ every integral in (A) will be zero and every integral in (B) will be π, so that $(A) \div (B) = \kappa_a' \div \kappa_a = 0.$

ELECTROMAGNETIC FIELDS DERIVED FROM NON-COMMUTING POTENTIALS

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In this note rules are given for deriving the components of the electric field, the magnetic field, and the current vector from an arbitrary q-number four potential. It is shown that from the mode of definition of these quantities it automatically follows that they satisfy a set of equations similar to Maxwell's equations and reduce to them for a set of mutually commuting potentials. The form of the equations with non-commuting potentials suggests a modification of the commutation laws for the electromagnetic field quantities given by Heisenberg and Pauli.[2] The new commutation laws are made to depend upon, or determine, as the case may be, the spatial distribution of charge and current. In the absence of matter the potentials and derived field quantities all commute. However, the use of a material particle as a test body to measure the field

quantities has the effect of introducing the proper uncertainties in them by the fact that non-commutativities between them must exist, due to the presence of the test particle.

Let A_0, A_1, A_2, A_3 be the components of an arbitrary q-number four potential. Let

$$p_a = \frac{h}{2\pi i}\frac{\partial}{\partial x_a} \qquad (a = 0, 1, 2, 3) \tag{1}$$

where $x_0 = -ct$ and x_1, x_2, x_3 are ordinary coördinates. We have

$$[p_a, f] = p_a f - f p_a = \frac{h}{2\pi i}\frac{\partial f}{\partial x_a}. \tag{2}$$

Let

$$P_a = \frac{h}{2\pi i}\frac{\partial}{\partial x_a} + \frac{e}{c}A_a = p_a + a_a. \tag{3}$$

We define the components E_k, H_k of the electric and magnetic fields respectively as follows:

$$\left.\begin{aligned} E_k &= \frac{2\pi ic}{eh}[P_0, P_k] \\ H_k &= \frac{2\pi ic}{eh}[P_{k+1}, P_{k+2}] \end{aligned}\right\} \quad \begin{aligned} &k = 1, 2, 3 \\ &P_{k+3} = P_k \end{aligned} \tag{4}$$

Expanding $[P_{k+1}, P_{k+2}]$ gives

$$\begin{aligned}[P_{k+1}, P_{k+2}] &= (p_{k+1} + a_{k+1})(p_{k+2} + a_{k+2}) - (p_{k+2} + a_{k+2})(p_{k+1} + a_{k+1}) \\ &= [a_{k+1}, p_{k+2}] + [p_{k+1}, a_{k+2}] + [a_{k+1}, a_{k+2}] \\ &= -\frac{h}{2\pi i}\left(\frac{\partial a_{k+1}}{\partial x_{k+2}} - \frac{\partial a_{k+2}}{\partial x_{k+1}}\right) + [a_{k+1}, a_{k+2}] \\ &= \frac{ihe}{2\pi c}\left\{\operatorname{curl}_k A + \frac{2\pi e}{ihc}[A_{k+1}, A_{k+2}]\right\}.\end{aligned}$$

Similarly

$$[P_0, P_k] = \frac{ihe}{2\pi c}\left\{\frac{\partial A_0}{\partial x_k} - \frac{\partial A_k}{\partial x_0} + \frac{2\pi e}{ihc}[A_0, A_a]\right\}.$$

Then (4) becomes equivalent to

$$\left\{\begin{aligned} E_k &= -\frac{1}{c}\frac{\partial A_k}{\partial t} - \frac{\partial A_0}{\partial x_k} + \frac{2\pi ie}{hc}[A_0, A_k] \\ H_k &= \operatorname{curl}_k A + \frac{2\pi ie}{hc}[A_{k+1}, A_{k+2}] \end{aligned}\right. \tag{5}$$

From the Poisson-Jacobi identity

$$[P, [Q, R]] + [Q, [R, P]] + [R, [P, Q]] = 0; \tag{6}$$

it follows immediately that

$$\sum_{k=1}^{3} [P_k, H_k] = 0 \tag{7}$$

which on expansion becomes

$$\text{div } H + \frac{2\pi ie}{hc} \sum_{k=1}^{3} [A_k, H_k] = 0. \tag{8}$$

Applying the Poisson-Jacobi identity in the form

$$[P_0 (P_{k+1}, P_{k+2})] + [P_{k+1}, [P_{k+2}, P_0]] + [P_{k+2}, [P_0, P_{k+1}]] = 0 \tag{9}$$

gives

$$[P_0, H_k] - [P_{k+1}, E_{k+2}] + [P_{k+2}, E_{k+1}] = 0. \tag{10}$$

On expansion this gives

$$\text{curl}_k E + \frac{1}{c} \frac{\partial H_k}{\partial t} = \frac{2\pi ie}{hc} \{[A_0, H_k] - [A_{k+1}, E_{k+2}] + [A_{k+2}, E_{k+1}]\}. \tag{11}$$

We define the charge density

$$\rho = -\frac{\pi c}{eh^2} \sum_{k=1}^{3} [P_k, (P_0, P_k)] \tag{12}$$

which on expansion gives

$$4\pi\rho = \text{div } E + \frac{2\pi ie}{hc} \sum_{k=1}^{3} [A_k, E_k]. \tag{13}$$

We define the components of the electric current as follows:

$$I_k = -\frac{\pi c}{eh^2} \{[P_{k+1}, [P_{k+1}, P_k]] + [P_{k+2}, [P_{k+2}, P_k]] + [P_0[P_0, P_k]]\} \tag{14}$$

which on expansion gives

$$4\pi I_k = -\frac{1}{c} \frac{\partial E_k}{\partial t} + \text{curl}_k H + \frac{2\pi ie}{hc} \{[A_0, E_k] - [A_{k+1}, H_{k+2}] + [A_{k+2}, H_{k+1}]\}. \tag{15}$$

The above definitions of ρ and I are useful because on applying the Poisson-Jacobi identity in the form

$$\{P, [Q, [Q, P]]\} = \{Q, [P, [Q, P]]\} \tag{16}$$

it follows that

$$\sum_{k=1}^{3} [P_k, I_k] = [P_0, \rho] \tag{17}$$

which on expansion becomes

$$\text{div } I + \frac{1}{c}\frac{\partial \rho}{\partial t} = -\frac{2\pi ie}{hc}\sum_{k=1}^{3}[A_k, I_k] - [A_0, \rho]. \tag{18}$$

Equations (8), (11), (13), and (18) become exactly Maxwell's equations and the equation of continuity of charge in the case where A_0, A_1, A_2, A_3 mutually commute with each other. Whether the extra terms in these equations drop out or not depends on the particular commutation laws satisfied by the A's.

If $\rho = I_1 = I_2 = I_3 = 0$ then it follows that

$$\sum_k [P_0, H_k^2] + \sum_k [P_0, E_k^2] = \sum_k [P_k, (E_{k+2}H_{k+1} + H_{k+1}E_{k+2} - E_{k+1}H_{k+2} - H_{k+2}E_{k+1})] \tag{19}$$

which when the potentials commute is Poynting's theorem. The extra term representing the rate of the field doing work on matter associated with the non-commutation of the potentials is

$$-\sum_k [A_0, H_k^2] - \sum_k [A_0, E_k^2] + \sum_k [A_k, (E_{k+2}H_{k+1} + H_{k+1}E_{k+2} - E_{k+1}H_{k+2} - H_{k+2}E_{k+1})]. \tag{20}$$

The form of equation (13) is of particular interest because if the density ρ of unquantized charge is zero we get

$$\text{div } E = \frac{2\pi e}{ihc}\sum_{k=1}^{3}[A_k, E_k]. \tag{21}$$

Therefore, if a single electron of charge $-e$ is fixed, at the place where the electron is we have

$$\frac{2\pi ie}{hc}\sum_{k=1}^{3}[A_k, E_k] = 4\pi e \tag{22}$$

or

$$\sum_{k=1}^{3}[A_k, E_k] = -2ihc, \tag{23}$$

and the left-hand side is zero at all other points in space. For complete symmetry

$$[A_k, E_k] = -\frac{2}{3}ihc\delta \tag{24}$$

where $\delta = 1$ at the electron and $= 0$ elsewhere. Heisenberg and Pauli give

$$[A_k, E_k] = -2ihc \qquad (25)$$

which holds at all points of space whether electrons are present or not. Equation (24) is of the right form for giving the proper uncertainties in the field quantities when measured by their effect on an immersed electron.

[1] NATIONAL RESEARCH FELLOW.

[2] *Z. f. Physik*, **56**, 1 (1929).

UNCOMPLICATED TRISOMIC INHERITANCE OF PURPLE VERSUS RED IN MATTHIOLA INCANA[1,2]

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Drosophila,[3] *Datura*,[4] *Lycopersicum*[5] and *Zea*[6] have each furnished one or more cases in which completely or partially triploid parents give ratios indicating that a particular gene locus is present in triplicate. In the trisomic "mutant" form of *Matthiola* which has been named *Narrow* (*Na*),[7] the extra chromosome evidently carries the locus of the genes *Bb*, which, in forms having sap color, determine the difference between purple and red, red being recessive.[8]

Narrow is frequently produced by normal parents belonging to the highly "mutable" race Snowflake, which has long chromosomes at first metaphase in the pollen mother cells.[9,10] A figure from an extracted F_2 long-chromosome plant, which shows the large extra chromosome of Narrow, has been published.[10] Trivalent formation has been observed, although, as in all other *Matthiola* trisomics studied, it does not occur regularly. Narrow seems to be a primary trisomic, carrying a complete extra chromosome of normal constitution.

Normal (diploid) plants of two red races (*CCRRbb*[8]) were crossed with trisomics (other than Narrow) of the white-flowered variety Snowflake (*CCrrBB*). Among the F_1 progeny (all purple-flowered) were several chromosome mutants of the Narrow type, and two of these ripened seed. Since both red races had short first-metaphase chromosomes, and presumably, therefore, seldom produced gametes with extra chromosomes, it is very probable that both these Narrows received the extra chromosome from the long-chromosome Snowflake parent.[10] It is therefore to be expected that, if the extra chromosome of Narrow carries the *Bb* locus, these F_1 Narrows would have the constitution *BBb*. If so, and if segre-

gation is random in the trisome, the expected F_2 ratios are: normals, 8 purple: 1 red; trisomics, 1 purple: 0 red.[4] The F_2 progeny of one F_1 Narrow (table 1) correspond closely to this expectation, and deviate very significantly from the 3:1 ratio usually found for purple vs. red in *Matthiola*;[11] the few progeny of the other F_1 Narrow are also close to the trisomic expectation. The one exceptional red among the F_2 Narrows can be explained either by crossing-over in the four-strand stage or by double non-disjunction in the second division without crossing-over.

TABLE 1

PURPLE AND RED PROGENY FROM SELFING OF HETEROZYGOUS PARENTS, INCLUDING TRISOMIC NARROWS ($2n$ + Na) AND NORMALS ($2n$) (NUMBERS IN PARENTHESIS CALCULATED FROM PROBABLE CONSTITUTION)

TRISOMIC TYPE AND GENERATION	PARENTAGE PROBABLE CONSTITUTION	INDIVIDUAL TESTED*	NORMAL PROGENY PURPLE	NORMAL PROGENY RED	TRISOMIC NARROW PROGENY PURPLE	TRISOMIC NARROW PROGENY RED
Narrow, F_1	*BBb*	Na 1	149	16	87	1
		Na 2	12	2	3	0
		Na 1 and Na 2	161	18	90	1
		(Same)	(159)	(20)	(91)	(0)
Narrow, F_2	*BBb*	Na 3	78	16	44	1
		Na 4	13	1	3	0
		Na 5	27	5	12	0
		Na 6	19	1	10	0
		Na 7	32	2	21	0
		Na 8	7	0	3	0
		Na 3 to Na 8	176	25	93	1**
		(Same)	(179)	(22)	(94)	(0)
Narrow, F_2	*Bbb*	Na 9	56	48	23	12
		(Same)	(58)	(46)	(27)	(8)
Normal, F_1	*Bb*†	N 1 to N 6	274	98	1	0
		(Same)	(279)	(93)	(0)	(0)

* "Na" indicates Narrow trisomics; "N" indicates normals. One Narrow F_2 parent giving only 3 progeny is omitted. All tested F_1 normals from the same two crosses as the Narrow parents are included. All progeny not positively determined are omitted; they were very few, aside from 26 plants in diseased cultures from parents Na 4 and Na 5, and their indications agree in trend with the data presented.

** Besides one red (omitted) that appeared to be a secondary of Narrow.

† Individual progenies ranged from 31 purple: 6 red to 72 purple: 38 red. The four normal parents from the same varietal cross as Na 1 gave 121 purple: 38 red.

The expectation for the constitution of the F_2 purple trisomics is: *2BBB*: *5BBb*: *2Bbb*. In F_3 (table 1), one F_2 parent gave a good approximation to the ratio expected from the constitution *Bbb* (normals, 5 purple: 4 red: trisomics, 7 purple: 2 red);[4] while the other six F_2 Narrows tested all gave progeny suggesting *BBb* parentage, with ratios for the combined totals close to expectation.

The ratios from normal parents (table 1) indicate ordinary disomic segregation for purple and red. With respect to the genes *Rr*, which determine the presence or absence of both sap color and pubescence in these crosses, the Narrow parents (table 2) gave ordinary disomic ratios, similar to those from the normal parents. Clearly the mechanism of segregation in the Narrow parents was normal in relation to the gene pair *Rr*, which is not linked with *Bb*.

TABLE 2

PUBESCENT AND GLABROUS PROGENY FROM SELFING OF THE PARENTS LISTED IN TABLE 1 (ALL HETEROZYGOUS FOR *R* AND *r*)*

	NORMAL PROGENY		TRISOMIC NARROW PROGENY	
PARENTAGE	PUBESCENT	GLABROUS	PUBESCENT	GLABROUS
Na, F_1	181	53	95	24
Na, F_2, *Bbb*	104	44	36	16
Na, F_2, rest	206	61	101	32
Na, F_2, all	310	105	137	48
Na, F_1 and F_2	491	158	232	72
Normal, F_1	373	136	1	0

* Including (1) the 1077 colored progeny reported in table 1, (2) 330 white-flowered progeny and (3) 56 plants recorded for pubescence but not for sap color. The grand totals, including 34 plants not positively determined as to trisomic type, are 1125 pubescent: 372 glabrous, the disomic expectation being 1123: 374.

The progeny ratios therefore conform to the expectation based on the hypothesis that the extra chromosome of Narrow carries the *Bb* locus, and that in the parents so far tested segregation occurred at random in the trisome. There is no indication that these ratios are modified by lethal action or by other differential viability. Thus this case seems to be a close parallel to that of purple vs. green in the Poinsettia trisomic of *Datura*,[4] and is in striking contrast to the complex situation presented by the trisomic inheritance of doubleness in *Matthiola*.

[1] Paper 251, University of California, Graduate School of Tropical Agriculture and Citrus Experiment Station, Riverside, California.

[2] The cytological evidence mentioned in this paper has been mainly obtained by Dr. Margaret Mann Lesley.

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THE PROBABLE ORIGIN OF OENOTHERA RUBRICALYX "AFTERGLOW" ON THE BASIS OF THE SEGMENTAL INTERCHANGE THEORY[1]

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Oenothera rubricalyx "Afterglow" has a circle of 8 chromosomes and 3 pairs in diakinesis. It falls on the basis of its breeding behavior into the group known as "half-mutants." Half-mutants produce but two classes of germ-cell, from the standpoint of genetic composition, one of which has a zygote lethal, and the other has no lethal. They have therefore an unbalanced lethal situation. As a result, half-mutants, when selfed, yield a progeny consisting of two-thirds repetition of the half-mutant, and one-third a pure homozygous form, which represents the alethal complex in double dose.

In a recent paper (1930), Dr. A. F. Blakeslee and the writer, attempting to show how a half-mutant may be formed from *Lamarckiana* as the result of a segmental interchange between the ends of opposing complexes, referred incidentally to the fact that the alethal complex of a half-mutant formed thus by segmental interchange cannot give the same arrangement of chromosomes in diakinesis with *both* complexes of the parent species (p. 229). If it gives a circle of 6 with one, it will give a circle of 8 with the other; if it gives a circle of 4 with one, it will give a circle of 10 with the other; if it gives 7 pairs with one, it will give a circle of 12 with the other.

Since that paper was sent to press, however, a paper by S. E. Emerson has appeared (1930), in which it is pointed out that the lethal-free complex of *rubricalyx* "Afterglow," known as ^{h}*latifrons*, when combined with the two complexes of *Lamarckiana*, *velans* and *gaudens*, yields a circle of 8 and 3 pairs with *both* of them. Assuming that Emerson's data are correct, it becomes necessary to explain this behavior of *rubricalyx* "Afterglow" on the basis of segmental interchange, if the theory is still to be regarded as a possible basis of half-mutant formation in Oenothera. That a satisfactory explanation can be found is indicated by the following paragraphs.

Let the complexes of *Lamarckiana* be arranged hypothetically in such a way that, with like ends uniting, the circle of 12 and one pair characteristic of this species is obtained, as follows (*gaudens* chromosomes belonging to the circle are in italics):

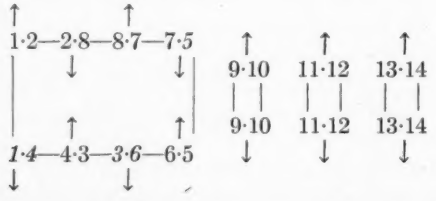
velans =	1·2	3·4	5·6	7·8	9·10	11·12	13·14
gaudens =	*1·4*	*3·6*	*5·8*	*7·10*	*9·12*	*11·2*	13·14

Now suppose that an interchange occurs between ends 2 and *8*. Then a half-mutant derived from the union of the modified *velans* complex resulting from this interchange with a normal *velans* complex would have the following formula (for reasoning, see Cleland and Blakeslee, 1931):

velans = 1·2 3·4 5·6 7·8 9·10 11·12 13·14 (has *velans* lethal)
modified velans = *1·4 3·6 5·2* 7·8 9·10 11·12 13·14 (has no lethal).

This half-mutant has a circle of 6 chromosomes and 4 pairs, and its alethal complex will give a circle of 6 with *velans*, and a circle of 8 with *gaudens*, if the mutant is crossed back with *Lamarckiana*.

Now all that is necessary, in order to obtain a form which will behave cytologically as *rubricalyx* "Afterglow" behaves, is for a further interchange to occur between ends 2 and 7 in the modified *velans* complex of this half-mutant. If this interchange occurred prior to the diakinesis stage in a spore mother cell, the cell in which the interchange occurred would have a circle of 8 chromosomes and 3 pairs, instead of the circle of 6 which is normally present in the spore mother cells of this plant:



The complexes resulting from disjunction of adjacent chromosomes of the circle in this cell would be:

velans = 1·2 3·4 5·6 7·8 9·10 11·12 13·14
twice modified velans = *1·4 3·6 5·7* 2·8 9·10 11·12 13·14

No crossing-over between complexes has resulted from this interchange. The *velans* lethal still resides, therefore, in *velans*, and the modified *velans* complex is still alethal. This twice-modified *velans*, if it united with a normal *velans* as a result of self-pollination, would produce a plant whose configuration would be a circle of 8 and 3 pairs, instead of a circle of 6 and 4 pairs. The modified *velans* of this plant would give a circle of 8 not only with *velans*, if the plant were crossed back to *Lamarckiana*, but would give the same configuration with *gaudens* (see above for formula of *gaudens*). Thus, we have, as the result of a single segmental interchange occurring in a primary half-mutant, the formation of a plant which follows the cytological and genetical scheme of *rubricalyx* "Afterglow." It has a circle of 8 chromosomes at the same time that it possesses a

modified *velans* complex associated with a normal *velans*, its alethal complex gives a circle of 8 with both *velans* and *gaudens*, when it is crossed back to *Lamarckiana*, and its breeding behavior is that of a typical half-mutant.

When now we ask what might be the ancestral form with a circle of 6, from which *rubricalyx* "Afterglow" has been derived by segmental interchange, our minds turn naturally to the only other *rubricalyx* known, a form with a circle of 6, and from which Shull's "Afterglow" has in all probability been derived. This is Gates' *rubricalyx*. It in turn has been derived from *rubrinervis*, from which it differs by a single unit character, possessing a dominant *rubricalyx* bud color factor. *Rubrinervis*, which also has the circle of 6, is a direct derivative from *Lamarckiana*, with the complexes, according to Renner, *velans* and a modified *velans* called *subvelans*. If our hypothesis is correct, therefore, *rubrinervis* is the primary half-mutant which has been derived from *Lamarckiana* by a single segmental interchange between a *gaudens* and a *velans* end. *Rubricalyx* Gates has been derived from *rubrinervis* probably by a gene mutation, which has left the end arrangement of the chromosomes undisturbed. *Rubricalyx* "Afterglow" has probably been derived from *rubricalyx* Gates by a further interchange between two ends of the modified *velans* complex.

In view of possible objection on the ground that *rubricalyx* "Afterglow" is contaminated with *grandiflora* or some other species, it may be well to emphasize the fact at this point that *rubricalyx* "Afterglow" is quite distinct in origin from the *rubricalyx* first studied by Shull, and the two strains should not be confused. Shull's first *rubricalyx* came from rosettes obtained from Dr. A. F. Blakeslee in 1912, who had grown them from unguarded seed received from Dr. R. R. Gates. "Afterglow," on the other hand, was obtained by Shull direct from Sutton & Co. in 1914, and came from carefully guarded and hand-pollinated flowers, in a generation not later than the second generation from the time when the strain, breeding true for *rubricalyx* pigmentation, was sold to this firm by Gates. The material from *unguarded* seeds was apparently contaminated with *grandiflora*. *Rubricalyx* "Afterglow," however, Professor Shull informs me, has never shown the slightest suggestion of contamination with *grandiflora* or with any other species. It seems safe to assume, therefore, that we are not dealing here with a situation where chromosomes 5·7 and 8·2 in the above hypothetical formula have been introduced from *grandiflora* or from some other species. Their presence in the *hlatifrons* complex is much more likely due to segmental interchange between non-homologous chromosomes of the modified *velans* complex of the original *rubricalyx*.

The chief importance of the above considerations lies not so much in the fact that they suggest a possible origin of *rubricalyx* "Afterglow," as it does in the indication which they give that the combined cytological

and genetical behavior of this form is *not* incompatible with the segmental interchange theory of circle formation in Oenothera.

Summary.—It is impossible for the alethal complex of a primary half-mutant derived from *Lamarckiana* by a single segmental interchange to give the same chromosome configuration with both complexes of the parent species. Nevertheless, a further segmental interchange between certain chromosomes of the alethal complex of the primary half-mutant may result in the formation of a secondary half-mutant, whose alethal complex *will* give the same chromosome configuration with both complexes of the original species, and whose behavior is thus like *Oe. rubricalyx* "Afterglow." The behavior of *rubricalyx* "Afterglow" in this respect is therefore not incompatible with the segmental interchange theory of circle formation in Oenothera.

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INHERITANCE OF BODY WEIGHT IN DOMESTIC FOWL

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For ten years the Rhode Island Agricultural Experiment Station has been conducting an extensive investigation to determine the mode of inheritance of growth rate and adult body-weight in the Light Brahma and Single Comb White Leghorn breeds of fowl and in their hybrids.

The two breeds used seem to be admirably adapted for a study of size differences. The Leghorn is a small breed, the female weighing approximately 1600 grams and the male 2000 grams at ten months of age. The Brahma is one of the largest breeds of domestic fowl. The Brahma female weighs approximately 3200 grams and the male 4000 grams at ten months of age. In weight variation the two breeds do not overlap. Males in all breeds of domestic fowl are significantly heavier than females. It is possible to approximate the male-equivalent weights of females at ten months of age by multiplying their recorded weights by 1.28. This correlation of female

weight with male weight allows the statistical treatment of the weights of both sexes as one group. But it is not applicable at ages prior to ten months for the ratio of female weight to male weight is not constant throughout the period of growth but varies from month to month.

In any quantitative study of size inheritance it must be demonstrated that the parent races are homozygous for the characters studied. This homozygous condition is best established in animals by observing the character in question on a large number of individuals preferably for several generations. The Leghorn strains used in the present investigation were bred together for seven consecutive generations, and the weight statistics of these Leghorns seem satisfactorily to establish the homogeneity of the Leghorn breed. The statistics obtained for the Brahma are equally convincing although the number of individuals is much smaller than in the case of Leghorns.

But the final test of the genetic weight constitution of the parents is found in their hybrid offspring. If the parent races are homozygous, we should expect, when they are crossed, to obtain fairly uniform hybrids, all of which should be of the same genetic character. If we obtain an intermediate condition in the reciprocal F_1 hybrids it means that they have probably received an equal influence from each of their parents regardless of which breed functioned as the male parent. The reciprocal F_1 hybrids studied are approximately intermediate between the weights of the parent breeds and the coefficient of variation for the hybrids is no greater than that of either parent. Thus, it is safe to assume that all of the F_1 individuals were heterozygous and genetically alike and the frequency distribution of all F_2 populations arising from F_1 parents should be the same. It has been established, beyond reasonable doubt, that all of the F_1 population, when crossed together do produce F_2 populations which are essentially similar. The coefficient of variability of these F_2 populations has in all instances been significantly greater than that of the F_1 population. This increase in variability in the F_2 renders probable the interpretation that segregation of some sort had taken place in the production of this generation. And this is supported by selected matings of small, intermediate, and large F_2 individuals.

In addition to the evidence of segregation afforded by selected matings of F_2 individuals, backcrosses of F_1 individuals with both parent breeds give evidence of a wide range of variation in the genetic constitution of the gametes formed by F_1 individuals.

An examination of the F_3 and F_4 matings will permit an explanation, in terms of definite Mendelian genes of the genetics of weight in this cross. The original small weight, as seen in the Leghorn breed, has in many instances been recovered in the F_2 generation. The same is true for large weight, though the evidence for this is not equally conclusive. Further,

these small weight and large weight individuals found in the F_2 population breed relatively true in subsequent generations.

This result enables one to estimate the number and stability of the genetic factors upon which weight in this cross is dependent. If typical Mendelian inheritance occurs, gene recombination should take place in the F_2 generation. The extent of this recombination would depend upon the number of genes operating, and the clearness of its demonstration would depend upon the number of offspring raised.

A working hypothesis has been adopted, based on the results obtained from a large series of selected matings, which will account satisfactorily for the inheritance of adult body-weight in this cross. The assumption has been made that the difference in weight between these two breeds is dependent primarily on two pairs of genes, each of which affects the weight of the individual equally and which together have cumulative effects. The evidence accords with this interpretation. On the other hand caution is necessary in suggesting that such very complex phenomena as weight are dependent upon a relatively small number of genes. Nevertheless, it is conceivable that a few genes may show a great influence on the growth rate and adult weight of an organism and that these few will more than equal in influence the combined or cumulative effects of many other genes. Such a situation, it is believed, exists in the present case and although the evidence presented in any one of the many matings would not by itself justify the hypothesis advanced, the combined data do justify its adoption.

In the groups of birds studied in this investigation it is shown that growth is a continuous process up to ten months of age, though at a steadily decreasing rate, the growth curve becoming convex upward subsequent to three months. At ten months growth is practically completed, such variations in weight as occur thereafter being due chiefly to accumulations or loss of fat.

Mature size is dependent upon two factors, (1) the rate at which growth takes place and (2) the duration of growth. The practical termination of growth comes at the same age; viz., ten months in both breeds studied and in their hybrids. Since initial hatching weight is substantially the same in all groups, and the duration of growth is the same, it follows that the differential genetic factors which influence adult weight must act through changes in the rate of growth. In other words, genes which influence adult weight do so through their effects on growth rate. A large bird has a relatively rapid growth rate at all ages, and a small one has a relatively slow growth rate at all ages. Birds of intermediate size have an intermediate rate of growth except when this is accelerated by heterosis, when their growth rate may temporarily exceed that of the large parent race.

Growth curve show clearly that at ten months of age Brahmas are approximately twice as heavy as Leghorns. This size difference holds for both

sexes. Further, all groups attain full growth at ten months of age. Growth of the larger breed is both at a higher rate and is more persistent, since the growth curve of Brahmas continues to rise steeply up to the tenth month, meeting its first conspicuous slowing up at nine months. On the other hand, the growth curve of the Leghorns both rises less steeply and is perceptibly slowed up a month or two earlier than is that of the Brahmas.

The F_1 and F_2 hybrids are heavier than either parent breed between the ages of three and thirteen weeks; subsequently they are closer to the Brahma than to the Leghorn breed up to about seven months of age, when their position becomes rapidly intermediate between that of the parent breeds, since the Brahmas continue to grow rapidly until ten months of age, while the Leghorns and hybrids grow slowly. The early growth of the F_2 hybrids is not as rapid as that of the F_1 hybrids although, as previously mentioned, the F_2 hybrids grow faster than the large Brahma breed up to the thirteenth week. Subsequently all the F_2 growth curves run parallel with but below the growth curve of the F_1 hybrids until adult weight is attained.

A study of the growth curves of the various F_3, F_4 and backcross groups shows that the genes which differentiate birds of a large breed from those of a small breed operate throughout the period of growth from hatching on. A genetically large bird grows not only more rapidly at all ages but more persistently than a genetically small bird. Hybrids occupy an intermediate position not only in mature weight, but also in rate of growth, except as this is modified by hybrid vigor.

Reciprocal crosses of Brahmas and Leghorns show no apparent effects of heterosis at ten months of age. The mean weight of the F_1 individuals is approximately intermediate between the weights of the parent races when growth is completed. Examination of the growth curves of the F_1 hybrids, however, shows that growth is greatly accelerated in the early stages surpassing that of the heavier (Brahma) breed. The growth curves of the F_2 hybrid groups rise above the curve of the Brahmas for the first three months after hatching but their superiority is much less than that of the F_1 group and terminates earlier. If hybrid vigor is the result of a heterozygous condition of allelomorphic genes it is to be expected that many of the F_2 individuals will be heterozygous for one or more genes and should therefore show heterosis. All F_2 segregates approaching a homozygous condition for large or small size should show little or no hybrid vigor.

The heterosis effect found in the F_1 hybrids is probably due not only to the two pairs of hypothetical weight genes, which at the most can involve only two of the reported 18 pairs of chromosomes of the domestic fowl, but also to many other genes involving possibly all the chromosomes. In the present investigation, however, it is of interest to determine to what extent the stimulating effects of hybrid vigor influence the average growth

rate of individuals known to approach a homozygous or heterozygous condition for the genes studied. It is to be supposed that the F_2 individuals are not all similar to the F_1 hybrids even for the two pairs of hypothetical size genes, many of them being heterozygous for only one pair of the genes or homozygous for both genes. Therefore, there is to be expected a decrease in the amount of hybrid vigor, although the average weight at ten months of age is approximately the same as in the F_1 group.

There can be no doubt about the occurrence of heterosis in the F_1 hybrids and to a lesser extent in the F_2 hybrids. To a lesser extent we should expect it to be present also in the F_3 and F_4 generations and it is probable that in general accelerated early growth when observed has this significance, though one cannot be certain of this in every case, since small numbers and peculiar seasonal or environmental conditions might give indications which were not significant. But in general there can be no doubt about the results. Where we expect theoretically a maximum of heterosis, in F_1 or in highly variable populations of later generations, we find the greatest acceleration of growth; where we expect little or no heterosis, in segregating high or low populations, or in those of intermediate character which show a low variability, little or no evidence of acceleration is found.

The effect of heterosis on early growth rate in the present cross of domestic fowl seems to support the hypothesis of G. H. Shull that a maximum amount of hybrid vigor is obtainable only when an organism approaches a completely heterozygous condition of all its allelomorphic pairs of genes. And when the organism approaches a homozygous condition there is a proportionate decrease in vigor.

A complete report of this investigation will appear in *Bulletin 228* of the Rhode Island Agricultural Experiment Station.